Volume XVII March, 1917 Number 28

TECHNICAL PUBLICATION NO. 8

OF

THE NEW YORK STATE COLLEGE OF FORESTRY

AT

SYRACUSE UNIVERSITY

HUGH P. BAKER, Dean

The Black Zones Formed by Wood-Destroying Fungi

BY

ARTHUR S. RHOADS

Published Quarterly by the University
Syracuse, New York

Entered at the Postoffice at Syracuse as second-class mail matter

COMMONWEALTH FORESTRY INSTITUTE
28 FEB 1955

Volume XVII March, 1917 Number 28

TECHNICAL PUBLICATION NO. 8

OF

THE NEW YORK STATE COLLEGE OF FORESTRY

AT

SYRACUSE UNIVERSITY

HUGH P. BAKER, Dean

The Black Zones Formed by Wood-Destroying Fungi

BY

ARTHUR S. RHOADS

Published Quarterly by the University
Syracuse, New York

Entered at the Postoffice at Syracuse as second-class mail matter

TECHNICAL PUBLICATIONS

OF

THE NEW YORK STATE COLLEGE OF FORESTRY.

To be had upon application by residents of the State.

TECHNICAL PUBLICATION No. 1, 1914.

Preliminary Report on the Diseases of Fish in the Adirondacks: A Contribution to the Life History of *Clinostomun marginatum*. By Dr. W. M. Smallwood. pp. 8–27.

No. 2, 1916.

I. A New Species of *Pityogenes*. By J. M. Swaine. pp. 8–10.

II. Observations on the Life History and Habits of *Pityogenes hopkinsi* Swaine. By Dr. M. W. Blackman. pp. 11–66.

No. 3, 1916.

The Development of the Vegetation of New York State. By Dr. William L. Bray. pp. 11–186.

No. 4, 1916.

The Relation of Mollusks to Fish in Oneida Lake. By Frank C. Baker. pp. 15–366.

No. 5, 1917.

The Hardwood Distillation in New York. By Nelson C. Brown.

No. 6, 1917.

Wood Utilization Directory of New York. By John Harris, Forest Service, revised and rearranged by Nelson C. Brown and Henry H. Tryon.

No. 7, 1917.

The Relation of Birds to the Western Adirondack Forest. By P. M. Silloway.

No. 8, 1917.

The Black Zones Formed by Wood-destroying Fungi. By Arthur S. Rhoads.

TRUSTEES

OF

THE NEW YORK STATE COLLEGE OF FORESTRY.

Ex Officio.

Dr. James R. Day, *Chancellor*	Syracuse University
Dr. John Huston Finley, *Commissioner of Education*	Albany, N. Y.
Hon. Edward Schoeneck, *Lieutenant Governor of the State*	Syracuse, N. Y.
Hon. George E. Van Kennen, *Chairman*, Conservation Commission	Ogdensburg, N. Y.

Appointed by the Governor.

Hon. Charles Andrews	Syracuse, N. Y.
Hon. Alexander T. Brown	Syracuse, N. Y.
Hon. John R. Clancy	Syracuse, N. Y.
Hon. Harold D. Cornwall	Lowville, N. Y.
Hon. George W. Driscoll	Syracuse, N. Y.
Hon. Francis Hendricks	Syracuse, N. Y.
Hon. Hendrick S. Holden	Syracuse, N. Y.
Hon. Louis Marshall	New York City
Mr. Edward H. O'Hara	Syracuse, N. Y.

Officers of the Board.

President	Hon. Louis Marshall
Vice-President	Hon. John H. Clancy
Treasurer	Hon. Hendrick S. Holden

FACULTY

OF

THE NEW YORK STATE COLLEGE OF FORESTRY

AT

SYRACUSE UNIVERSITY.

HUGH POTTER BAKER, M. F. (Yale 1904), D. Oec. (Munich 1910),
Dean of the College; Professor of Silviculture.

FRANK F. MOON, B. A. (Amherst 1901), M. F. (Yale 1909),
Professor of Forest Engineering.

MAULSBY WILLETT BLACKMAN, A. B. (Kansas 1901), Ph. D. (Harvard 1905),
Professor of Forest Entomology.

EDWARD F. McCARTHY, B. S. (Michigan 1911),
Professor of Forestry at the New York State Ranger School, Wanakena, N. Y.

NELSON COURTLANDT BROWN, B. A. (Yale 1906), M. F. (Yale 1908),
Professor of Forest Utilization.

J. FRED BAKER, B. S. (Michigan Agrl., 1902), M. F. (Yale 1905),
Director of Forest Investigations.

LEIGH H. PENNINGTON, A. B., 1907, Ph. D. (Univ. of Michigan 1909),
Professor of Forest Pathology.

SEWARD D. SMITH, B. S., M. F. (Michigan 1910),
Director of State Ranger School.

JOHN WALLACE STEPHEN, B. A. (Michigan 1907), M. S. F. (1909), M. Pd. (Michigan Normal College 1915),
Professor of Silviculture.

CHARLES CHRISTOPHER ADAMS, B. S. (Illinois Wesleyan 1896), M. S. (Harvard 1899), Ph. D. (Chicago 1908),
Professor of Forest Zoology.

HENRY R. FRANCIS, B. S. (Massachusetts Agrl. 1910),
Professor of Landscape Extension.

SHIRLEY W. ALLEN, B. S. (Iowa State 1909),
Professor of Forest Extension.

HARRY P. BROWN, B. A. 1909, A. N. 1910, Ph. D. (Cornell 1914),
Professor of Dendrology.

REUBEN PARKER PRICHARD, B. S. (Dartmouth 1907), M. F. (Yale 1909),
Assistant Professor of Forest Products.

LAURIE D. COX, A. B. (Acadia 1903), S. B. in Landscape Architecture (Harvard 1908),
Assistant Professor of Landscape Engineering.

RUSSELL TAYLOR GHEEN, B. S. F. (Pennsylvania State 1912), M. F. (The New York State College of Forestry 1914),
Assistant Professor of Forest Extension.

HOWARD BLAINE WAHA, B. S. (Pennsylvania State 1909),
Assistant Professor of Forest Engineering.

HENRY HARRINGTON TRYON, A. B., M. F. (Harvard 1913),
Assistant Professor of Forest Utilization.

WILLIAM O. ELLIS, A. B. (Lebanon Valley 1911), M. S. (Iowa State 1913),
Instructor in Forest Entomology.

ALAN F. ARNOLD (Harvard),
Instructor in Landscape Engineering.

ARTHUR S. RHOADS, B. S. F., M. S. (Penn State 1913, 1914),
Assistant in Forest Botany.

ALVIN G. SMITH, M. S. (New York State College of Forestry 1915),
Field Assistant in Forest Investigations.

LILLIAN M. LANG,
Secretary to the Dean.

MILDRED E. WOOD, B. L. E. (Syracuse 1914),
Librarian.

WALTER W. CHIPMAN (Wabash 1893),
Cashier.

ELIZABETH CONE,
Recorder.

PREFACE

The chemical changes which occur in wood as the result of fungal activity are very imperfectly understood. The records of nearly all the work that has been done are in German and many of them are practically inaccessible. The present publication is an attempt to throw some light upon the nature and significance of so-called "Black Lines" or zones of decay which accompany the activity of several species of fungi in many kinds of wood. In this attempt use is made of all available published work, which is analyzed and discussed in the light of the observations and experiments which the author himself has made. It is not claimed that the problem is solved but this publication gives some new light upon the subject and opens the way for continued investigation of this important question. Further investigations upon this and other problems of timber decay are now under way in our laboratories.

L. H. PENNINGTON.

Digitized by the Internet Archive
in 2025

https://archive.org/details/technical-publication-state-uni-ny-college_1917-03_17_28

THE BLACK ZONES FORMED BY WOOD-DESTROYING FUNGI.

ARTHUR S. RHOADS.

INTRODUCTION.

Various phases of pathological study have occupied the attention of botanists at different times. Before the causes of diseases in plants where known the general external appearance of the affected organ was described. Later most of the attention was directed toward the discovery of the parasitic organisms which cause the derangements, and incidentally the study of the physiologic responses of the host plant was begun. Within the last few years many students of the subject have examined various morphological changes which occur in diseased plants, first dealing almost entirely with the gross anatomic appearance, but later making more minute histological and cytological investigations. Woody tissue when invaded by fungi, however, is just beginning to be studied carefully. Moreover, comparative studies are always helpful in deciding general principles. Only as we become acquainted with many examples of cytological and histological changes can we arrive at the truth regarding the reaction of the host plant to parasitic invasion. The practical value of such results can hardly be doubted.

To combat a disease successfully we should know as much as possible about the causes. We should therefore understand the pathologic reactions of the diseased plant. The relations between parasitic fungi and their host plants are of various kinds. Here we largely confine our attention to the effects of the fungus upon its host and, among these, we are

principally concerned with those changes which disturb the normal physiologic processes.

For several years the black zones found in decaying wood have been a subject of much conjecture. Briefly stated, the problem resolves itself to this. In the early stages of the decay of dicotyledonous woods by many of the higher fungi known as "polypores," characteristic blackish zones, limiting various stages of the decay, occur as prominent features of the decomposition. These zones may extend in any direction through the wood or bark, their courses being determined by the initial starting point of the fungus and its subsequent growth and advancement through the wood. Their occurrence may be observed best on the cross sections of a tree or log which is but partially decayed. Here they usually appear as blackish or brownish-black lines of varying thickness (Plate 1). Strictly speaking, the term "line" should not be applied to these formations unless used in describing their appearance on a section of wood, since it is only when seen in this manner that they appear as lines. In reality they are thin zones of discolored wood which at first sharply separate the various stages of decay in the wood (Plate 1). If, however, the decay starts from several centers, so that the decayed areas overlap, the figure becomes complicated and the dark zones extend very irregularly throughout the whole mass (Plate 2). The course of the discolored zones of wood is in no way influenced by the course of the growth rings. It usually runs parallel to the direction of the woody elements, although there is considerable variation in this respect.

Microscopic examination shows these discolored zones to be caused by brown infiltrations in the cell walls and lumina of the cells. These infiltrations frequently become so abundant that they exude into the lumina of the cells, particularly the vessels, and occlude these completely (Plate 4, Fig. 1). This brown substance usually forms a blackish zone or layer but frequently appears merely as a brown discolora-

tion in the wood. When seen in mass it is responsible for the dark coloration mentioned above. At the start the coloring material is a liquid but later dries to a brown amorphous substance. It is presumed that this brown substance consists of decomposition products that have infiltrated into the wood immediately in advance of the encroaching mycelium of the fungus.

In addition to the decomposition products associated with the activities of wood-destroying fungi, the formation of a similar substance has been observed to take place in the tissues of dicotyledonous trees exposed through wounds and as yet free from fungal attack. More recently attention has been called to the formation of similar substances in dead branches and fallen woody parts of dicotyledonous trees, even before they become attacked by wood-destroying fungi. In such trees, sections made through the wounds a few days after their formation show that brownish globules of a gum-like substance occur abundantly in the vicinity of the wounded area. These globules, commonly termed "wound gum" by the earlier writers, eventually flow together into larger ones which fill up the lumina of the woody elements, particularly the vessels, thereby protecting them to a certain extent against injurious influences. This protective effect, however, is not sufficient for absolute security against the decomposition and decay of the exposed wood. On this account wound diseases are much more likely to occur in dicotyledonous trees than in the conifers, for the resin secreted by the latter quickly flows out over the surface of the wound and excludes the entrance of air and fungi.

So far as the writer has been able to ascertain, this problem never has been made the subject of an investigation by anyone in this country. The presence of this discoloration is noted invariably in the majority of our descriptions of the decay of dicotyledonous woods. Beyond merely noting the occurrence of these zones of infiltrated wood, but little has

been done toward the study of them. Occasionally they have been alluded to in slightly greater detail by a few authors in this country. On the other hand many valuable investigations carried on during the last quarter century by German workers, to explain closely related subjects, have thrown considerable light upon our problem. For the establishment of many important principles I am indebted to the writings of Dr. Ernst Münch which have been used as a basis for a portion of this paper, since the writer firmly believes that his explanation of the origin of this infiltration and its physiologic significance is the ultimate one. For this reason, and in order that the results of his investigations may be brought to the attention of those in this country who may be interested in them, a number of his results and experiments that deal with our question have been quoted.[1]

HISTORICAL.

It is first necessary to review briefly the older literature dealing with the pathologic changes which, originating in the region of wounds in wood, are accompanied by a brown discoloration and are termed, according to their position and arrangement in the stem, "protection wood," "protection heart," "false heart," "pathologic heart," and etc. Frank (1895, p. 31)[2] states that the woody plants, without exception, exhibit the phenomenon of a darkening to a considerable

[1] This study was started in the Botanical Laboratory of The Pennsylvania State College under the direction of Prof. C. R. Orton, to whom the writer is indebted for advice and through whom he became interested in the problem. Grateful acknowledgment is hereby made of my indebtedness to Dr. William Frear and Dr. Guy Given of the Experiment Station for their instruction and advice upon the chemistry of the problem. Further investigation was carried on in the Botanical Laboratory of The New York State College of Forestry. The writer also wishes to express his gratitude to Dr. L. H. Pennington and Dr. H. P. Brown for many helpful suggestions and criticisms, both of the work and the manuscript.

[2] Bibliographic citations in parentheses refer to "Literature Cited," pp. 46-49.

depth of the tissue exposed through wounds. In cross sections of such wounds this is especially noticeable in as much as the discolored tissue is sharply differentiated from the underlying unchanged woody tissue. Microscopic examination shows that this darkening is due to the fact that the cell walls of the wood in question have been discolored by a brownish substance. Especially have the lumina of the vessels and the adjoining cells become filled up with a solid mass of brown material. Frank has named this brown material "wound-gum."[3] In the tissues thus modified, in the vicinity of wounds tyloses arise in most dicotyledonous woods. These are bladder-like outgrowths of the parenchyma cells which project into the vessels and occlude them quite effectually. We find the vessels partly filled with "wound-gum" and partly filled with tyloses.

Robert Hartig (1878), in his work on the diseases of wood, explained this browning as the first step in the decomposition of the wood or of wound decay. He stated (pages 66 and 140) that the dark brown discoloration of the decayed wood is due to the fact that a yellow or brownish liquid is contained within the woody elements. This liquid substance, upon drying, collects as a crust upon the cell walls or as a brittle yellow or brownish substance which cracks in various directions and completely fills the cells. He considered this substance to be a humus solution and stated that it consists of the decomposition products of the cell contents which have been dissolved in the water that leaches in from without and penetrates farther into the wood.

[3] This substance has no connection with the true gum which arises through the secretion of the cell walls of stone fruits and tropical gum trees and which, in every respect, is of a different nature. Similar material has been called "protection gum" and "wood gum" by other authors. Theodor Hartig and certain later authors have used the word "Kernstoffe" which the writer has translated to the term "decomposition products" and used throughout this paper to avoid ambiguity and for the sake of uniformity.

In opposition to R. Hartig's conception, Frank (1884) stated that these brown masses of wound-gum in the darkened areas — likewise the tyloses — are products of living wood parenchyma. He reasoned that their formation is due to a universal life process to afford protection by excluding outside air from the living wood so that the natural functions of the latter are thereby kept undisturbed. He therefore called the wood thus darkened "protection wood." Frank stated further that its formation can be induced artificially by wounding and that one can cause it to be produced at any desired position in a living tree. According to Frank the protection wood is anatomically and physiologically identical to the heartwood which is to be found in most dicotyledonous trees after a certain age. The benefit which the tree receives through the closing of its woody elements to the outer air by the "protection wood" lies, according to Frank, mainly in the fact that the air within the wood becomes independent of atmospheric pressure.

Temme (1885), working under Frank's direction, found an increase in the specific gravity of the "protection wood" over that of the sapwood. He stated that the penetration of air and rain water through open vessels hastens the disintegration of the wood and also maintained that the wood browned by the infiltration of decomposition products offers a certain protection against destruction. From his experience in the care of trees, Temme concluded that the customary covering of the smaller wounds with tar or tree wax was superfluous, since they are closed temporarily by the protective wood until they are healed over, after which they are closed permanently.

It must be emphasized, however, that considerable credit is due to Böhm (1879) who had disclosed all of the essential features of protection wood several years before. He observed (p. 224) that the pathological transformation to heartwood occurs predominatingly at the boundary between living

and dead wood. Even before Böhm, Theodor Hartig (1857) and others had concerned themselves with the most important phenomena of normal and pathologic heartwood formation as well as the chemical reactions of the infiltrating decomposition products.

Gaunersdorfer (1882) likewise contributed to this subject. He studied (principally on *Syringa*) a brown zone of protection wood in wounded twigs, established its similarity to normal heartwood, and made a careful examination of the brown infiltration. His results indicate a noticeable increase in weight for the pathologic heartwood. The physiologic significance of the protection wood is to retard or render impossible the harmful atmospheric inflow into the deeper-lying living tissue. It would seem, therefore, that the protection wood has an important function to fulfill. He assumed that the infiltrating substance is produced from living cells, chiefly from the starch grains. He, as well as Böhm, believed that the occlusion of wounds by the infiltration of the wood constitutes a safeguard against injurious external atmospheric influences.

Opposed to this von Tubeuf (1886) found in *Cytisus* that wood transformed to pathologic heartwood is easily penetrated and destroyed by fungal threads. Therefore he contested the idea that a protection is instituted against destruction and stated that the transformation of the margin of the wound to pathologic heartwood did not render the artificial closing of the wound unnecessary as had been claimed by the earlier authors. For the remainder von Tubeuf leaned toward Böhm's theory. In his opinion pathologic heartwood formation, subsequent to wounding, is a reaction against oxidation and pressure changes and, in specific cases, perhaps against fungal ferments. He confirmed R. Hartig's observation that all pathologic heartwood cells are dead.[4]

[4] Further literature, the discussion of which would take too long, is given by von Tubeuf (1899).

The subject of pathologic heartwood formation received additional light through the investigation of the false heart of red beech by Hartig and Weber (1888). Normally the red beech does not form heartwood, even in old age. In many cases, however, brown discolorations start from branch wounds and spread through the interior of the trunk, often extending throughout its whole length. In this reddish-brown heart the vessels are occluded by tyloses and there are drops of gum in the parenchyma cells and other elements. It is stated that the increased entrance of air through the branch wounds permits an increased activity of the living parenchyma cells. This is shown by the formation of tyloses and wound gum in the parenchyma cells. It was observed that fungal mycelium also occurs frequently in the dark brown heart. The false heart is to be considered as pathologic and does not differ essentially from genuine heartwood.

Hermann (1902) confirmed the opinion of R. Hartig on the origin of the false heartwood from branch wounds. He also found fungal mycelium present in nearly all cases. The false heartwood was considered as a protection by the tree against the entrance of wood-destroying fungi into the wounds. The fungal hyphae are at first occluded from air and moisture by the tyloses and masses of gum, and their development retarded. The tyloses and gum formations ultimately are dissolved by the penetrating fungal hypae.

Tuzson (1903) arrived at similar conclusions. He stated that the tyloses and wound gum occur in the heartwood merely in consequence of the stimulation by the fungus and not as a reaction against the entrance of air after wounding. He found that the red heartwood is more resistant to fungi than the sapwood. The observation that a similar formation of false heartwood also occurs in felled wood attacked by fungi is important. Tuzson found that the formation of false heart increases the specific gravity of the wood.

Some work of Lindroth (1904), which is also based upon

the protection wood theory, is of more importance. Lindroth investigated the pathologic heartwood (the protection wood of Frank) found in a thin zone surrounding portions of wood decomposed by *Polyporus nigricans* Fries. Such pathologic heartwood proved to be rich in infiltration products and thereby increased in weight, hardness, and durability. He stated that this infiltrating substance arises through the combined action of the fungus in the rotten heartwood, and the oxygen of the air. The pathologic heartwood was considered by him to retard the progress of the fungal decomposition.

To sum up these rather diversified results of the earlier workers, the brown substance commonly occurring in the vicinity of wounds in wood is to be considered as a secretion of the parenchyma cells. This substance is said to have the function, either in conjunction with the tyloses or in their absence, of occluding the severed vessels. By this means the air in the tissues is rendered independent of the atmospheric pressure. In this manner the tissues are protected against the entrance of fungi and consequent decay. The cells are stimulated to form tyloses and decomposition products by means of fungal hyphae, wound stimulus, entrance of oxygen, and pressure changes. The discolored wood is denoted, according to its position in the stem, as protection wood, false (pathologic) heart, or protection heart (when surrounding wounded areas). It is said to be similar to normal heartwood.

Münch (1910[2]) arrived at somewhat different results by which he very clearly settled the differences of opinion existing among the earlier authors. His results concern, first of all, the origin of the brown substance, the decomposition products, arising in the protection wood. He states that this substance is not a secretion of living cells but that it arises only after the death of the cells as an oxidation product of the cell contents.

Münch states that when tyloses occur in pathologic heartwood along with the decomposition products they have an entirely different method of formation and cause than do the decomposition products. It is his belief that they arise earlier while the woody elements are still alive, as outgrowths of the same. He attributes their formation to the entrance of air through a wound, that is, to wound stimulus.[5] Moreover, these stimuli result in an increased transportation of nourishment into the living tissues surrounding the dead (infiltrated) portions of wood. If these enriched portions of the wood are killed afterwards and infiltrated, the false heart thus produced has (according to Münch) an appreciably higher specific gravity than normal wood. The occlusion of the vessels retards the ready access of external air. Therefore the paucity of oxygen within the tissues of living wood renders it less penetrable to fungal hyphae.

ORIGIN OF THE DECOMPOSITION PRODUCTS (KERNSTOFFE).

The earlier authors did not agree as to whether the decomposition products (wound or protection gum) arise as a secretion product of living cells or as an oxidation product of the dead cells. Frank's statement that the cells furnishing the decomposition products are living during the formation of such substances never has been proved and it must suffice to consider his theory as wholly hypothetical. Even Frank's work does not appear to justify this statement and it appears from it and still more from similar investigations by Will (1899) that the formation of decomposition products cannot be the result of a vital process. Frank (1884, p. 323) described the microscopic details of wound gum formation

[5] According to Münch (1910[2]) tyloses also occur at points where the entrance of air is excluded and the stimulus afforded by fungous excretions or decomposition products must be accepted as the reason for their origin.

as follows. In the vicinity of the margins of wounds a reddish discoloration was observed after 8 to 10 days. This is due to a coloration of the cell walls, especially those of the pith rays. In these cells brown drops (the wound gum) arise as a new formation of the cell contents and partly as a transformation of the starch grains. Their formation then continues farther. The brown substance infiltrates the cell walls and eventually exudes into the lumina of the vessels, partly occluding them. From this description it does not appear that Frank's view is justified for, as Münch (1910[2]) has stated, a "browned" tissue, the parenchyma cells of which are filled with brown material, is necessarily dead and therefore incapable of further vital activity. In such tissue described by Frank, if the formation of the brown substance continues, then it can hardly be a question of a secretion of living cells.

It is difficult to understand how anyone can consider such changed and discolored cells to be alive. The investigations of Böhm, R. Hartig, von Tubeuf, and later those of Münch (1910[2]) have shown, beyond all possible doubt, that the cells furnishing the decomposition products are always dead. Münch found that the formation of the brown product occurred in dessicated cells as well as those infected by fungal hyphae — cells which were unquestionably dead.

There is no further foundation for asserting that the decomposition products arise from living parenchyma cells other than the following account of Frank (1884, p. 330) in which he states that the gum formation as well as the formation of tyloses is truly a vital process and not a purely chemical process of disintegration. This follows from the fact that it does not occur in fallen trees and branches as soon as they are dead. Münch (1910[2]) declares this to be wrong and states that under certain circumstances there arises in fallen, doubtlessly dead, woody parts a brown material which, according to its appearance, origin, and chemical reactions,

may be designated as Frank's wound gum. In order to prove this he made detailed studies of poplar (*Populus balsamea*) twigs, in which he allowed unpeeled twigs to dry out in a room so that generally from one to two weeks elapsed before they showed signs of dessication. He observed that death naturally took place first in the vicinity of the cut ends and that the bark and outermost portions of wood likewise died before the deeper-lying ones which were better protected from drying. The protoplasm became rigid and lost its fine granular structure; in addition the most of it turned a light brown. In the twigs, soon after the death of the parenchyma cells, there occurred a darkening of the wood and especially of the bark. Münch furthermore determined that the dark color originated exclusively from the brown substance which was present in the parenchyma cells and that the darkening appeared first in the parts which were more affected by the drying, that is, at the ends and at the periphery. Thence it proceeded rapidly toward the center of the twig.

Upon making radial sections at the place where only the outer part of the wood was darkened and the inner was still white, Münch observed that the pith ray cells at the boundary between these two areas contained several brown globules. He found that all the cells, even the inner ones which were still uncolored, had died and did not respond to the plasmolysis test. Farther toward the outside scattered brown droplets were noticed in the vacuoles of the protoplasm. In the cells situated near the periphery of the twig these brown droplets had coalesced to form larger drops. These frequently contained several small bubbles. Münch states that examination of such cells showed unmistakably that the liquid contents of the vacuoles suddenly become changed at some time after the death of the cells to brown viscid drops which became firm and hard after coalescing. In wood that was still further dried he observed cracks in some of the individual brown globules.

These brown globules, according to the illustration and description given by Münch are identical in appearance and chemical properties with those observed by the writer in the sapwood of a log of pignut hickory, *Hicoria glabra* (Mill.) Britton, attacked by a common sap-rot fungus, *Coriolus prolificans* (Fries) Murrill. Radial sections (10 microns) were made of portions of wood which were in the first stage of decay — that is, the wood had been penetrated by fungal hyphae but disintegration had not started. The portions which were sectioned consisted of small resistant areas of wood (Plate 3) left intact after the remainder of the sapwood of the log was completely decomposed. These areas were sharply demarked from the surrounding, almost completely decayed wood by prominent black zones. In these radial sections almost all of the pith rays contained abundant brown droplets (Plate 4, Fig. 2).

According to Münch the brown substance in the pith ray cells of the poplar twigs examined by him is identical with that spoken of by Frank (1884) as wound gum and by Th. Hartig (1857) as "Kernstoffe," since it possesses all of the characteristic chemical properties mentioned by Th. Hartig and Frank and has a similar origin. Münch finds it to be insoluble and to remain unchanged in water, alcohol, ether, concentrated caustic potash, concentrated sulphuric acid (in which the wood swelled up and became darker), and cold concentrated nitric acid. In boiling concentrated nitric acid he observed that the brown substance quickly dissolved to a colored solution. The latter reaction had been reported earlier by Th. Hartig (l. c.), who had first studied the substance.

Frank (1884, p. 324) in describing the characteristics of wound gum states that if a cross section of such infiltrated wood be digested for a quarter of an hour with dilute hydrochloric acid and potassium chlorate the gummy substance is converted into a new compound which, while likewise in-

soluble in water, is readily soluble in alcohol. Continued digestion with this reagent, however, finally dissolves the gummy substance completely. Münch found that this reaction took place in the substance with which he worked, especially when the mixture was hot; with a cold mixture, as a rule, a greater time was required.

Münch (1910[2]), however, considers it an error of Frank, which had not been disputed previously, that this reaction (alcohol solubility after digestion with hydrochloric acid and potassium chlorate) is a particular characteristic for wound gum. He is of the opinion that the same reaction probably also occurs with starch-containing cells which do not show the slightest trace of browning or gum formation. As proof of this Münch treated thin sections of the inner, absolutely white, living sapwood of *Prunus avium* and *Fagus sylvatica* for ten minutes in the above-mentioned mixture. After this treatment the rich starch contents changed into clear drops which, upon the addition of alcohol, disappeared instantly under the microscope. He found that the same behavior was exhibited by the contents of the bark cells regardless of whether they were living and colorless or dead, browned, and filled with the brown substance. From the action of such strong reagents, however, he failed to draw any conclusions as to the nature of the substance.

According to Münch (1910[2]), the brown congealed product of the cell contents arises not only in cells killed by dessication but likewise in cells killed by other causes. The recognized browning caused by fungal attacks originates generally from such substances only, in this case, they are less isolated and in general occur mixed with the cell contents (remnants of the protoplasm). Moreover, they are present here mostly in slight quantity because the constructive product, the cell contents material, has already been partially consumed by the fungus. In order to prove this Münch examined poplar twigs which he infected while living with *Stereum pur-*

purcum. In these he found, in the vicinity of the hyphae growing nearest the vessels, that the protoplasm of the parenchyma cells was dead or nearly so. It had contracted from the cell walls and gave slight or no further plasmolysis with suitable reagents. The remaining cell contents had collected as colorless drops which were soon browned and mixed with the dead protoplasm so that the pith rays *en masse* appeared brown. Even here the brown substance gave all the reactions recorded for wound gum except that the resistance against the use of cold hydrochloric acid and potassium chlorate was many times greater than that given by Frank. Münch was convinced that even in this case of death through fungi — the brown substance arises only after the death of the cells but never, however, in living tissues. He observed this clearly by microscopic examination of infected living twigs and pieces of wood, especially in those cases in which he permitted fungal hyphae to grow over the surface of living wood in a moist chamber. In this case he could easily follow the advance of the fungus and the browning. It was evident to him that the latter does not precede the fungous attack but appears only at some distance behind the growing, pointed hyphae where the sound wood cells had been killed by the fungus.[6] He concluded that the browning therefore can not be a preventive measure, a means of protection of the plant against fungous attack.

According to Münch (1910[2]) the substances which furnish the decomposition products may leave the cells, after the death of the protoplasm, and exude into the lumina of the vessels. For this, however, a greater quantity of cell sap is required than is at the disposal of the drying poplar twigs. He believes that the oxidation of these products occurs mostly in the vessels which are rich in oxygen. The oxidation of

[6] According to Münch it is different in living trees where the fungal ferments become distributed by the sap-flow and can then act injuriously upon distant-lying cells.

these products results in the formation of the brown drops which later become solidified and occlude the vessels. Moreover, in coniferous woods which are killed by fungi the brown drops occurring in the parenchyma cells are, to all appearances, of the same nature and manner of origin.

With regard to the transformation of the cell contents of coniferous woods, Münch cites an experiment by which he could follow, microscopically, the entrance of a bluing fungus, *Endoconidiophora coerulescens*, into the parenchyma cells of pine wood. He made thin radial sections from living pine wood and placed them in hanging drops in van Tieghem cells, the whole being done under sterile conditions. In the case cited the reserve material consisted entirely of fat in the form of a fine emulsion in the protoplasm. If no infection followed he noted that such cells in a hanging drop culture remained unchanged for several days. If, on the contrary, viable fungous spores were inoculated into the drop culture he observed that the conditions changed at once. As soon as the fungal hyphae reached a pith ray they promptly invaded it, ramified, and soon filled the cells completely. He observed that the fine granular structure of the protoplasm immediately disappeared into the cells attacked and the contents flowed together into drops. Upon careful observation, minute thin-walled fungal hyphae were always to be found in the cells thus altered. These drops were still colorless at the end of the experiment and were (as Münch learned by comparison of other tests of wood killed by such fungi) similar in every way to those previously described by Frank except that they did not become brown. That this substance can also occur in the parenchyma cells of coniferous wood had been found previously by Will (1899).

The writer has never observed nor could any reference in literature be found concerning the occurrence in coniferous woods attacked by wood-destroying fungi, of the prominent blackish zones which are characteristic features associated

with certain decays of dicotyledonous woods. Similar formations are characteristic of the decay of spruce and larch caused by *Poroduedalea pini* (Thore) Murrill, but they are inconspicuous when compared to the broad zones of decomposition products which commonly occur in the decay of dicotyledonous woods. Such decomposition products arising through the decay of coniferous woods by wood-destroying fungi apparently are small in quantity compared with those arising through the decay of dicotyledonous woods. Why we have such a condition is not known.

If the decomposition products in question were dependent upon the hemicellulose, xylan (wood gum), for their source we might have a plausible explanation of this peculiar circumstance. According to Storer (1898) the evidence thus far accumulated tends to show that the wood gum in the trunks of trees is, comparatively speaking, difficult of digestion and less active, physiologically speaking, than the true cellulose with which it is accompanied and combined. In proof of the small quantity of wood gum obtainable from coniferous wood by the direct action of alkaline solutions, Thomsen (1879, p. 159) says that, unlike the wood of dicotyledonous trees which give up to dilute soda lye from 8 to 26 per cent of wood gum, fir wood is hardly at all acted upon by soda lye. He obtained less than 0.8 per cent of wood gum from spruce wood and less than 0.5 per cent from fir wood. In these coniferous woods he states that wood gum appears to be present only in minute quantities. Other authors have come to similar conclusions in regard to the wood gum content of other coniferous woods.

The great differences in structure between coniferous and dicotyledonous woods suggests another plausible reason for the discrepancy between the relative amounts of decomposition products arising through the decay of these respective classes of woods. In the dicotyledonous woods, owing to the presence of much larger elements — the vessels — we should

naturally expect to have an increased flow of air through the wood, thereby permitting a much more rapid and complete decomposition than could possibly occur in coniferous woods.

In order to be entirely certain that the decomposition product is produced in cells that are attacked by wood-destroying fungi, Münch conducted an experiment in which he placed pieces of fresh beech sapwood in closed sterilized chambers and observed them for several weeks. He noticed that these wood samples developed tyloses profusely; in the cambium region even a luxuriant growth of callus began. However, the familiar brown coloration betraying the formation of the decomposition products did not appear, the surface of the wood merely coloring to a pale yellowish brown. If, on the contrary, the pieces of wood were inoculated with a wood-destroying fungus the discoloration, indicative of the decomposition of the cell contents into a brown substance, arose immediately in all parts killed by the fungus. There can therefore be no doubt that the brown drops, designated by Frank as wound gum, are a decomposition product of the cell contents and that they occur only in dead cells.

The striking fact that the cell contents, which are without question very easily oxidized, do not experience oxidation in the cells even where there is a free transmission of air through the wood is to be explained by the properties of the living protoplasm. With the death of the protoplasm by drying, frost, heat, fungous attack, etc., its permeability is destroyed. As a result the air flows in upon the vacuole contents which are no longer protected and oxidation of the cell contents occurs.

The presence of moisture is as necessary to the oxidation described as it is for most chemical decompositions of that nature. According to Münch, in the case of the poplar twigs for example, if the dessication be greatly hastened by removing the bark and drying in a hot room, no browning occurs. In this case, after the death of the protoplasm by dessication,

he believes that the twigs lose their moisture too rapidly for the browning to follow. It is also known in other cases that rapid removal of water prevents browning. The prompt drying of pressed plants obviates the dark coloration; fruit dried quickly retains its bright color. Münch (1910[2]) has stated to the contrary, however, that in many kinds of wood (beech, etc.) no browning occurs even when the drying is gradual. On the other hand he finds that the browning does not occur if the necessary degree of moisture but insufficient oxygen is present. According to the same authority, wood that is very rich in water and therefore poor in oxygen remains uncolored for a long time. The fact follows that the absence of browning is no proof of freedom from fungous attack.

Bailey (1910) investigated the discoloration of sapwood, or "sap-stain" as it is called commonly, which occurs on freshly cut surfaces of certain dicotyledonous woods. He found that when freshly cut surfaces of such woods were exposed to the air under favorable conditions of temperature and moisture a chemical reaction started which, with varying rapidity, produced a colored substance in the wood. The examination of microscopic sections of this sap-stained lumber revealed the fact that the colored substance produced by the chemical reaction was most conspicuously developed in the pith rays and wood parenchyma cells, living tissues which are largely concerned in the storage and conduction of food in the wood. Bailey points out further that in general sap-stain is the result of two agencies: the attacks of fungi and chemical discoloration, the latter being caused in the sapwood by the activity of oxidizing enzymes. That both agencies are closely related to the food substances available in the wood is shown by the fact that the discoloration, whether produced by the activity of fungi or by chemical reaction, is most conspicuously developed in the pith rays and wood parenchyma cells. In addition both agencies producing sap-stain are de-

pendent upon atmospheric oxygen, heat, and water in certain proportions. According to Bailey the optimum conditions for sap-staining are found in green timber during hot humid weather, whereas unfavorable conditions are found in cold dry weather and in logs immersed in water.

It is generally known that if fungous-infected wood be exposed to the air for several hours its surfaces turn brown. This is especially striking in woods that normally are white. Lindroth (1904) has made observations of this nature on sections of birch wood decayed by *Polyporus nigricans* Fries. He marked the outer limit of a dark zone on a section with a lead pencil and after keeping the wood in a moist chamber for 15 hours observed that a new discolored zone had formed outside of the pencil mark. He concluded therefore that the formation of this new discolored zone occurred through the combined action of the atmospheric oxygen and the fungus. That the oxygen alone did not cause this is obvious because sound birch wood does not become colored so rapidly when exposed to the air under the above conditions. That, on the other hand, the fungus alone did not cause the new discoloration he confirmed since the dark zone could only be found within a few millimeters of the exposed surface.

As Münch (1910[2]) correctly stated, the formation of the brown decomposition product is dependent upon the concurrence of three factors, the presence of dead cells, an optimum supply of moisture, and a sufficient supply of oxygen to promote oxidation. This makes it clear why the so-called protection wood formation is often confined to a very definite zone, namely directly at the boundary between dead and living wood.[7] In Münch's opinion it would be far more con-

[7] In addition to the above-described formation of the decomposition products resulting from the oxidation of the cell contents Münch (1910[2]) observed that the mycelium of certain fungi excreted drops of a substance which, upon microscopic examination and microchemical tests, apparently was identical with that arising in the parenchyma cells of

ceivable that similar brown oxidation products may be formed from substances which occur in the free cell sap. In some instances, however, as in cherry wood, the large amount of substance infiltrated in the vessels cannot be attributed to the contents of the parenchyma cells but must come from some other source — possibly the cell wall.

Modern researches have shown that a number of hemicelluloses occur as carbohydrate reserve materials which are deposited in the form of thickened cell-walls in the endosperm of seeds and as secondary layers of thickening in the wood parenchyma and wood prosenchyma elements of certain woods. By means of enzymes these reserve materials may be converted into gums and sugars, in which form they may be transported to those parts where growth is taking place. The investigations of Grüss (1896) have shown that a cell-wall which consists of a mixture of two hemicelluloses, is dissolved fractionally by the action of a cytolytic enzyme, that is, one constituent earlier than the other. He found further that the hemicelluloses araban and galactan were transformed respectively into the gums arabin and galactin which could be transported to tissues even before they were further changed into the sugars, arabinose and galactose. Grüss finds that these gums occur in the dormant reserve materials of the genera *Acacia*, *Astragalus*, *Prunus*, and others, and denotes them as reserve gums. He finds that the result of oxidizing enzymes on the hemicelluloses is to effect a partial digestion of this assimilation product, by which sugar and gum is formed, the amount of gum varying with the completeness of the digestion. After the resolution of the hemicelluloses into sugar and gum the sugar is leached out while the gum is left behind. Grüss is of the opinion that this

---

wood as an oxidation product of their cell contents. He states further that, while possible, it is extremely improbable that substances similar to oxidation products of the cell contents may be excreted by fungi in certain woods.

enzymatic digestion of the hemicellulose reserve materials is the explanation for the phenomenon of gummosis.

As was stated earlier, the hemicellulose, xylan, is difficult of digestion and less active physiologically than the true cellulose with which it is accompanied and combined. After this hemicellulose is converted into sugar and gum by enzymatic action, it is not impossible that the gum may be further changed by an oxidative or other action into an insoluble by-product while the sugar is utilized as food by the fungal hyphae.

RELATION OF PATHOLOGIC AND NORMAL HEARTWOOD.

All who have concerned themselves with the question of the relation of pathologic and normal heartwood have considered them from the anatomic and physiologic standpoints. In normal heartwood formation it is to be supposed that the inner, older parenchyma cells have died normally through age, lack of function, deficient food supply, etc., and that their contents, in part at least, seep through the cell walls and even ooze out into the lumina of the neighboring cells. The normal heartwood is also to be regarded as an initial stage of decomposition when considered in this limited sense. Where tyloses occur they may be considered to have arisen from the parenchyma cells which remain alive longer than the other elements. The older sapwood is always poorer in water and richer in air than that last formed. It has been found that heartwood, normal as well as pathologic, has greater specific gravity and is richer in solid substances than the sapwood. The transformation to heartwood therefore must be regarded as an addition to the woody substance due to the oxidation of the cell contents and the decomposition of these residues within the woody elements.

It must be remembered that, in the case of pathologic heartwood near wounds in living trees, an increase in weight has

been established only for those portions transformed to heart which lie on the outer surface of the wounded tissue. Here the tyloses and infiltrated decomposition products are most abundant, often in such quantity that an increase in material is evident by mere macroscopic observation. These parts are easily recognized macroscopically by their darker color. They either surround, as "protection heartwood," portions of wood less strongly transformed to heartwood or they bound wound surfaces as "protection wood." In these cases this zone of "protection wood" is distinguished from the dead wood which it isolates, only by the fact that the tyloses and the oxidation products are more abundant. Hermann (1902) has already mentioned this as occurring in the pathologic heartwood of beech.

An explanation of this remarkable accumulation of brown material in the uninjured tissues directly underlying dead wood in wounded areas is furnished by the discovery of Münch (1910[1], p. 389). He has pointed out that wherever woody or bark tissues are killed there is an extraordinary movement of formative materials toward the neighborhood of the dead area as a result, so that in such places the cambial activity may be increased several times and additions to the bark may occur beyond the normal. According to the same author the living parenchyma cells in the neighborhood of dead cells have a special attractive force for the formative materials and consequently an increased growth and subdivision may occur, which often is manifested in a prolific formation of tyloses. So, for example, when the fungal hyphae penetrate and consequently kill a portion of the wood an abnormal stream of building materials then flow into the tissues adjoining the dead areas and the parenchyma cells involved develop tyloses. The parts previously rich in these substances are killed likewise by the advancing fungus and its diffusing enzymes. The cell contents are oxidized, after which the transformation to pathologic heartwood is complete.

As Münch (1910[2]) states, it is therefore clear that an important accumulation of materials occurs, especially in those places where the drying is gradual or where the penetration of the disease-producing organism is very slow as, for example, in the periphery of the decayed areas. Here the wood cells have the maximum time to attract material to them before they in turn become attacked and killed by the fungal secretions or other injurious influences. It is not impossible that even after death a woody portion may be enriched by the flow of substances from the surrounding, living cells due to purely physical causes and, upon the concentration of such substances the deposition of them as solid materials may occur within the areas concerned. Otherwise the frequently described accumulations of calcium carbonate and calcium oxalate in plant tissues would be difficult to explain. However, this is to be regarded as a hypothesis less well established.

Such increase of substance as a result of pathological heartwood formation has been investigated by numerous workers. Lindroth (1904) stated that the infiltrated decomposition products formed in birch wood, as a result of its decay by *Polyporus nigricans* Fries, imparts great hardness to the wood and retards the decomposition of the same. He stated that while the specific gravity of the sound wood was 0.99, that of the dark infiltrated zone was 1.23. By absolute dry weight he found the specific gravity of the sound wood was 0.77 while that of the dark zone was 0.90.

THE PHYSIOLOGIC SIGNIFICANCE OF THE DECOMPOSITION PRODUCTS.

Many investigators have observed that the fungal hyphae do not appear to be able to penetrate the heavier infiltrations of decomposition products occurring as blackish zones demarking decayed from undecayed areas of wood. Consequently they have attributed a protective effect to this forma-

tion. Lindroth (1904) in discussing such a zone of "protection heart," as he called it, caused by *Polyporus nigricans* Fries in birch wood, states that it is especially resistant to decomposition and offers a certain protection against further attack by the fungus. If it should happen, as these blackish zones continue to become thicker, that the supply of water within the diseased portions of the wood falls below the demand made upon it by the fungus, the mycelium — providing it has not been smothered in the meantime — may break through and transform another zone into pathologic heartwood. This gives rise to the well-known concentric blackish zones which at first sharply separate the various stages of the decay in wood (Plate 1).

It is plausible that the occlusion of the vessels and other elements of the wood renders the pathologic heartwood, as well as the healthy wood lying directly without it, relatively free from air; furthermore it inhibits the circulation of air and hence the inroads of the fungal hyphae. It is also possible that the brown decomposition products with which the cell walls frequently are infiltrated may be, to a certain degree, harmful to fungi. At least such infiltrated substances are more difficult for them to assimilate than those constituents which have not yet been oxidized. Owing to this the contents of the cells which otherwise would be an important source of nitrogen for the growth of fungi have assumed through chemical decomposition a form more difficult to assimilate. On these grounds greater resistance to decomposition by fungi is to be expected, especially if the fungi which have caused this transformation to pathologic heartwood are already smothered. For fungi coming in later the culture medium is made poor.

Under optimum conditions for the growth of fungi, heartwood (normal as well as pathologic) in its typical condition is more highly resistant to decay than the sapwood. In a living tree, however, the sapwood frequently is less attacked

than the heartwood, a condition often resulting in hollow trees. This condition generally occurs from the absence of oxygen in the sapwood in consequence of its large amount of water. As soon as the moisture ratio between the heartwood and the sapwood is upset, as in dead or felled wood, the sapwood which (owing to its greater abundance of food materials) is by far the more favorable medium for the growth of fungi and is decomposed much more quickly than the heartwood.[8] Von Schrenk (1900, p. 48) has observed the readiness with which the sporophores of many wood-destroying fungi can be induced to form wherever a wound is made in the diseased trunk, thus admitting air. As we now know, the decomposition of woody tissue occurs through the combined action of fungal hyphae (by virtue of their enzyme excretions), water, oxygen, and a favorable temperature. The entrance of air alone does not destroy the woody tissue and in the absence of sufficient air and moisture the fungal threads, which decompose the wood, cannot function.

Decomposition very seldom occurs from small surface wounds in trees or in the cut ends of small branches because here the injured woody portions are sufficiently protected by the absence of air in consequence of the large water content of the sapwood. The conditions are otherwise where the deeper-lying tissues of larger limbs or the trunk are exposed, since these are better aerated. In the latter case fungal hyphae penetrate, following the vessels and pith rays, and ramify in the center of the stem. The result is that tyloses are formed in the vicinity of the wounded areas where the wood is still living. Later, after the death of the parts attacked, the browning of the contents of the parenchyma cells (formation of decomposition products) occurs. As has been shown, both of these formations are to be seen most frequently in the regions immediately adjoining the infected areas,

[8] Compare the investigations of Tuzson (1903, p. 16) and those of Münch (1910[2]) which agree in the essential points.

especially where the advance of the fungus is very slow or almost stopped. The portions of the wood thus changed have been designated as "false (pathologic) heart." Münch (1908, p. 44) is of the opinion that the small supply of air in the interior of the tree as a rule suffices only for a slight growth of the fungus. This causes merely a browning of the wood cells without affecting the woody substance to any great degree. If larger wound surfaces are left unprotected the air in the deeper-lying tissues is constantly renewed (Münch, 1908, p. 44). The fungus may then continue its existence and work of decay. Thus the "false heart" is transformed into heart-rot. The same author (1910[2]) states further that the renewing of the air by means of diffusion and diosmosis, which varies according to the greater or less porosity of the wood and from other reasons, plays an important role. From this it follows (according to Münch) that the oxygen streaming in from the outside in a radial direction toward the heart or in the intercellular spaces of the pith ray cells is respired by the living sapwood cells, either partially or entirely. Therefore it is merely the remainder of the oxygen left after respiration that is available for the fungus living in the heart. In his opinion more or less oxygen is admitted to the attacked heart, according to the intensity of the respiration, the number of wood cells, etc. Nothing more definite can be ascertained concerning this matter until our knowledge of the vitality of the wood cells is increased.[9]

It is appropriate that the question of what eventually becomes of the decomposition products as the decay progresses be discussed briefly at this point. The writer has observed frequently in the case of the decay of logs of pignut hickory, *Hicoria glabra* (Mill.) Britton, and other woods by *Coriolus proliferans* (Fries) Murrill, that the decomposition products

[9] Compare the conclusions of Münch (1910[1]).

disappear with the completion of the decay. Von Schrenk (1914), in discussing the decay of lilac (*Syringa vulgaris* L.) stems by *Polystictus versicolor* (L.) Fries, says that the brown substance is destroyed ultimately when the decay nears completion. The decomposition products, which have been shown to originate with the advancement of the fungus through the sound wood, are likewise destroyed by the fungus upon the completion of the decay in a given area and no traces of them are left in the completely decomposed wood. Evidence of this is to be found in that the decomposition products at first are always present in a thin zone between the decayed and undecayed wood. Later when the decay spreads from several centers the decomposition products collect in thin zones between the various areas of wood in different stages of decay. Thus the constant association of these blackish zones of decomposition products with that portion of the sound wood bordering upon the decayed wood is to be explained by the fact that they are destroyed upon the completion of the decay within any one area but new ones constantly form from the sound wood as soon as it is attacked by the advancing fungus.

There remains to be considered the identity of those substances from which the decomposition products are formed, the chemical changes taking place, and the final chemical nature of the brown decomposition product. The present study has not been sufficiently extensive to answer these questions fully. Here we are entering a little known field since, even at the present time, but little has been achieved as to the chemical composition of sound wood and virtually nothing concerning the chemical changes which accompany its decay.

It is evident, however, that the cell contents and possibly certain other substances originally combined with cellulose and lignin to constitute the cell wall furnish the formative material which, through oxidation in the presence of moisture, coagulates to thick drops and gives rise to the decom-

position products which ultimately infiltrate certain portions of the wood, giving rise to blackish zones.

CHEMICAL NATURE OF THE DECOMPOSITION PRODUCTS.

The indefinite and complex group of substances formed by the partial decomposition of vegetable matter is generally called "humus" and so long as the word is used in a collective sense as a convenient term it may be retained. From its general properties we may infer that "humus" is a slowly oxidizable colloid varying in color from brown to black. Unfortunately we cannot get much farther at the present time. The partially decomposed material of woody plants forms a particularly vague and indefinite group of substances containing all the non-volatile products of fungal, enzymic, and oxidative reactions on the plant residues. A detailed study of this group being thus out of question we must first ascertain what part it bears to the original woody substance and then, when we know what to look for, try to discover what particular constituents of the woody plant enter into its formation.

These decomposition products which subsequently infiltrate certain portions of the wood are exceptionally resistant to chemical reagents. Heald (1906) in discussing the deposits of it in cottonwood due to *Elfvingia megaloma* (Lév.) Murrill, states that it is evidently insoluble in alcohol, ether, caustic soda, caustic potash, hydrochloric acid, and only slightly soluble in strong nitric acid.

Stevens (1910, p. 367) states that wound gum may be found lying free in the dead cytoplasm, surrounding starch grains which have contributed to the formation of the gum-like substance. He gives the properties of wound gum as follows: "Wound gum is not soluble in warm water, but may be dissolved in hot nitric acid or in eau de Javelle after several hours. It is not soluble in sulphuric acid, potassium

hydrate, alcohol, or ether, but may be dissolved in alcohol after treatment for a few minutes with a solution of potassium chlorate in dilute hydrochloric acid. It may be stained with a solution of fuchsin, iodine green, safranin, or methyl green. It is stained red by phloroglucin and hydrochloric acid." The writer has observed that the previously described drops formed in hickory wood by *Coriolus prolificans* (Fries) Murrill, also may be stained by these respective reagents.

According to Temme (1885) wound gum agrees with many sorts of gums in that it yields oxalic and mucic acids on oxidation with nitric acid. It differs essentially, however, from all gums in not swelling in water and in being insoluble even in caustic potash and sulphuric acid. As has been recognized by Temme, wound gum is stained deep red by phloroglucin and hydrochloric acid. Molisch showed later (1888, p. 264) that it behaves just like lignified membranes in aniline sulphate, metadiamido-benzol, orcin and thymol; and he believes that wound gum contains vanillin in solution.

Tests upon radial section (10 microns) of the wood shown in Plate III, these sections being identical with those shown in Plate IV, Fig. 2, were made to determine the solubility of these decomposition products. The solubility tests were made by exposing thin sections to the action of the reagent (without heating) in watch glasses, meanwhile making observations with the microscope. If the numerous globules of the decomposition products, which are readily visible in the pith ray cells under the low power of the microscope, did not dissolve after a reasonable length of time a small quantity of the reagent and sections were transferred to a test tube, heated to the boiling point, and again examined under the microscope. The globules of decomposition products were found to be insoluble in water, concentrated ammonium hydroxide, 10 per cent solution of sodium hydroxide, 10 per cent solution of potassium hydroxide, and concentrated hydrochloric acid. In cold concentrated sulphuric acid the wood

was carbonized but the globules remained intact. Upon heating the acid to boiling the wood dissolved together with more or less of the decomposition products. In cold concentrated nitric acid the decomposition products were insoluble but upon heating to boiling the wood dissolved together with the globules, forming a brown solution. Moreover, tests performed with other sections indicated that the decomposition products in question were insoluble in absolute alcohol, xylene, acetone, ether, petroleum ether, chloroform, carbon bisulphide, and carbon tetrachloride. In addition to this, sections of the wood containing the globules of decomposition products were placed in a concentrated solution of chloral hydrate and kept at a temperature of 55 degrees C. for one week. There was no effect other than a slight swelling of the globules. The same sections were then washed in water and dehydrated by alcohol. Part of them were treated with clove oil and the remainder with cedar oil, but the decomposition products remained insoluble in both cases.

An attempt was made to determine more fully the chemical nature of the decomposition products by means of a comparative analysis of sound and decayed wood. Sapwood of a log of pignut hickory, *Hicoria glabra* (Mill.) Britton, which was partially decayed by *Coriolus prolificans* (Fries) Murrill, was used in the study of the decayed wood and sapwood from a living tree of the same species (gathered in the spring) for the sound wood. In the case of the decayed wood a thick black layer of infiltrated wood sharply demarked the completely decayed wood from the small areas of sound wood remaining, these areas being only in the first stage of decomposition (Plate III). This black layer, as well as the wood enclosed by it, was very hard. The infiltrated wood was shaved off carefully, care being taken not to include the underlying, uninfiltrated wood. [10] The sound sapwood also

[10] The completely decayed wood that surrounded those pieces of wood which remained intact within the log, was scraped off carefully before they were photographed.

was reduced to shavings and, after thorough drying, both samples were ground finely.

These samples of finely divided wood were first successively submitted to a preliminary extraction, without heating, for 24 hours with ether, 95 per cent alcohol, a 10 per cent solution of sodium hydroxide, and a 5 per cent solution of hydrochloric acid so that, when the decomposition products were extracted finally they would be free from many extraneous substances. Parallel tests were conducted on equal quantities of infiltrated wood and of the normal sapwood. The ethereal and alcoholic filtrates, in both cases, contained such exceedingly small amounts of substance that they were not further investigated. The alkaline filtrate from the sound wood residue, upon the addition of 90 per cent alcohol, gave a characteristic precipitate of xylan (wood gum). The alkaline filtrate from the infiltrated wood, however, upon the addition of 90 per cent alcohol gave a brown flocculent precipitate which, judging from its solubility and other chemical reactions, consisted of a mixture of two or more substances — at least very little wood gum was present. After the alkaline extraction the woody residues were washed and then subjected to extraction with a 5 per cent solution of hydrochloric acid for 24 hours. The acid filtrates thus obtained were practically colorless and the woody residues, in both cases, apparently remained unchanged. After this extraction the one from the infiltrated wood was, as far as could be determined by microscopic examination, as darkly colored as it was at the beginning of the original treatment.

Both the woody residues were then subjected to the action of an oxidizing agent (hydrochloric acid and potassium chlorate) after which, according to Temme (1885) and Frank (1884), the decomposition products are rendered soluble in alcohol. Münch (1910[2]), however, considers that Temme and Frank are in error for giving this reaction (alcohol solubility after digestion with hydrochloric acid and

potassium chlorate) as a characteristic of wound gum and shows that starch-containing cells which do not exhibit the slightest browning or gum formation likewise respond to this reaction. They did not continue to investigate the chemical nature of the brown decomposition product beyond finding that it was soluble in alcohol after digestion with a mixture of hydrochloric acid and potassium chlorate. This has been one of the chief objects of the present study.

Both the residues were then digested by boiling in a mixture of hydrochloric acid and potassium chlorate (5 gms. of potassium chlorate to 100 cc. of 80 per cent hydrochloric acid) for 15 minutes. The woody residues from this oxidizing treatment, after thorough washing, were compared. It was found that neither was destroyed by the strong oxidizing action but the residue from the infiltrated wood had lost all of its original blackish color and was only slightly darker than that from the sound wood. When examined under the microscope the cells of the ground infiltrated wood appeared to be filled with a light, reddish brown substance, while the cells of the sound wood also appeared to contain a similar substance but in smaller quantity. Both the oxidizing liquors left from this treatment were brown in color and when neutralized with sodium hydroxide gave brown precipitates respectively, the one in the case of the sound wood being the darker. These precipitates were not investigated further since they were deemed not to be of any material importance.

The woody residues left from the oxidizing treatment were then submitted to a cold extraction with absolute alcohol for 24 hours. In both cases the alcohol instantly assumed a brown hue due to material entering into solution. This treatment seemed to take most of the coloring substance from both woods, although the residues responded slightly to a second and even to a third extraction. The alcoholic filtrates were evaporated to dryness and weighed. Roughly estimated, about twice as much material was obtained from the infil-

trated wood as from the sound wood. Both residues were dark brown in color and exhibited a conchoidal fracture. The one from the infiltrated wood was of the deeper hue.

Both alcoholic extracts were insoluble in cold or boiling water, concentrated hydrochloric acid, ether, petroleum ether, chloroform, carbon bisulphide, and carbon tetrachloride. Their specific gravities are indicated by the fact that they were not suspended in or floated upon any of the organic solvents tried of which the heaviest, carbon tetrachloride, has a specific gravity of 1.63. Neither, however, sank in concentrated sulphuric acid, whose specific gravity is 1.84. Both alcoholic extracts, however, were soluble in cold absolute alcohol, acetone, and a 10 per cent solution of sodium hydroxide. When the last named solution was neutralized with sulphuric acid the extracts, in both cases, were precipitated — that is to say they were insoluble in the exactly neutral sodium sulphate solution thus prepared. Both alcoholic extracts were soluble to a brown solution, but dissolved more slowly and without carbonization, when shaken in cold concentrated sulphuric acid. The alcoholic extract from the infiltrated wood was soluble in cold ammonium hydroxide, whereas that from the sound wood was soluble only by heating the reagent to boiling. When hydrochloric acid was added to the ammoniacal solutions until they were slightly acid both extracts were precipitated, leaving the solutions colorless in both cases.

None of the treatments thus far applied have secured a separation of the substances peculiar to the infiltrated wood and giving to it its distinguishing color. The solubilities and other properties of the respective extracts indicate that they are, for the most part, made up of like substances and in the case of the infiltrated wood, in addition to the materials originally present in the sound wood, there is present one or more decomposition products which, for a time at least, are little or not at all affected by the fungus producing the decomposi-

tion. The similarities of the substances decomposed by the oxidizing treatment, as regards solubility and behavior toward other reagents except the oxidizing reagent, show relationship between the original materials and the decomposition products here in question. The solubility relations of both indicate that, before oxidation, they would be classed with the hemicelluloses, but that they are so altered by oxidation as to become soluble, particularly in alcohol and acetone without losing their insolubility in sodium hydroxide and in acidulous salt solutions.

SUMMARY.

1. The brown substance commonly occurring in dicotyledonous woods attacked by wood-destroying fungi is indicative of the first stage of the decomposition of the wood.

2. The formation of a similar and probably identical substance also occurs in wounds of living dicotyledonous trees and, under certain circumstances, in fallen woody parts where fungous growth may not be present. This is to be considered as due solely to oxidation of the woody substance without the stimulus afforded by the presence of wood-destroying fungi which would greatly hasten the decomposition.

3. Both decomposition products arise only after the death of the cells through the oxidation of their contents and certain constituents of their walls. This formation occurs most notably in the parenchyma cells.

4. The decomposition products formed in the decay of dicotyledonous woods infiltrate the cell walls to a greater or less extent, frequently becoming so abundant as to form numerous brown drops within the lumina of the cells. Such deposits appear in the wood as blackish zones of varying thickness which occur at first between decayed and undecayed areas and later separate areas in different stages of decay. Wood thus infiltrated is to be considered as pathologic heartwood.

5. The blackish zones are not constant in position since the decomposition products, which cause the discoloration, move forward with the advance of the decay in any part of the stem and ultimately disappear upon its completion within that part. The continual occurrence of the blackish zones between decayed and undecayed wood is due to the fact that the decomposition products are destroyed together with the wood while new ones are formed constantly from the wood as fast as it is attacked by the advancing fungus.

6. In the decay of coniferous woods the formation of decomposition products of similar nature to those studied here is very small in quantity as compared with those arising in the decay of dicotyledonous woods.

7. The formation of the brown decomposition products is dependent mainly upon the concurrence of three factors: (a) the presence of dead cells, (b) an optimum supply of moisture, and (c) a supply of oxygen sufficient to promote oxidation.

8. The partially decomposed material of woody plants forms a particularly vague and indefinite group of substances containing all the non-volatile products of fungal, enzymic, and oxidative actions on the plant residues. The resultant products are exceptionally resistant to chemical reagents.

9. It is evident that the cell contents and certain other substances, particularly the hemicellulose xylan (wood gum), that originally were combined with the cellulose to constitute the cell wall furnish the formative material which, through oxidation upon the entrance of air and the presence of water, coagulates to thick drops and gives rise to the decomposition products which ultimately infiltrate certain portions of the wood, causing them to appear as blackish zones.

10. In the wood of the pignut hickory the hemicellulose xylan (wood gum) is destroyed early in the progress of the decay. In the early stages of the decomposition of the wood (in that portion infiltrated with the decomposition products

and appearing as a blackish zone) the wood gum, in its partially oxidized state, apparently is the substance which is responsible for most of the discoloration. Later, however, when the blackish zones advance and the decay becomes completed within that portion of wood which the decomposition products formerly occupied, the wood no longer responds to chemical tests for wood gum.

11. By the action of a strong oxidizing reagent on fresh sapwood a brown decomposition product can be prepared artificially which is essentially like that occurring naturally in dicotyledonous woods, whether in wounded areas of living trees, dead wood, or as the result of the action of wood-destroying fungi.

12. After subjecting both sound and infiltrated wood to the action of a strong oxiding reagent and extracting the products whose nature was changed by the action, the chemical properties of the respective extracts indicate that they are, for the greater part, made up of like substances. In the case of the infiltrated wood in addition to the materials originally present in the sound wood there is present one or more decomposition products which are temporarily left little or not at all affected by the fungus producing the decomposition. The solubility relations of the extracts obtained from both woods indicate that, before oxidation, they would be classed with the hemicelluloses but that they become greatly altered in nature by the action of the oxidizing reagents.

13. The decomposition products whose formation is due to the action of wood-destroying fungi have proven to be a group of substances analogous to or nearly identical with the decomposition products which arise under certain circumstances in dead wood that is entirely free from fungous attack and which have been known under the name "wound gum." Their formation is greatly accelerated by the presence of wood-destroying fungi which greatly hasten the decomposition and hence the oxidation.

LITERATURE CITED.

Bailey, Irving W.

1910. Oxidizing enzymes and their relation to "sap stain" in lumber. Bot. Gaz., **50**: 142-147.

Böhm, Joseph.

1879. Über die Function der vegetabilischen Gefässe. Bot. Ztg., **37**: 225-239; 241-258.

Frank, A. B.

1884. Über die Gummibildung in Holze und deren physiologische Bedeutung. Ber. d. D. Bot. Gesell., *2:* 321–332. Abs. *in* Bot. Centbl., **20**: 194–196.

1895. Die Krankheiten der Pflanzen. 2nd Aufl. p. 31. Breslau.

Gaunersdorfer, J.

1882. Beiträge zur Kenntniss der Eigenschaften der Kernholzes. Sitzungsber. d. Ak. d. Wiss. [Vienna], **85**: 9.

Grüss, Johannes.

1896. Über Lösung und Bildung der aus Hemicellulose bestehenden Zellwände und ihre Beziehung zur Gummosis. Bibliotheca Botanica **39**: 1–13, pl. 1.

Hartig, Robert.

1878. Die Zerstezungserscheinungen des Holzes der Nadelbäume und der Eiche in forstlicher, chemischer und botanischer Richtung. 151 pp., 21 tab., Berlin.

Hartig, Robert, and Weber, Rudolf.

1888. Das Holz der Rothbuche in anatomisch — physiologischer, chemischer und forstlicher Richtung. p. 31. Berlin.

Hartig, Theodor.

1857. Beiträge zur physiologischen Forst-Botanik. Allgem. Forst- u. Jagd. Zeit., 1867: 281-296.

Heald, F. D.

1906. A disease of the cottonwood due to *Elfvingia megaloma*. Nebraska Agr. Exp. Sta. Rept., **19**: 92–100, pls. 1–4.

Herrmann.

1902. Kernbildung der Buche. Ztschr. f. Forst- u. Jagdw., **34**: 596.

Lindroth, J. Ivar.

1904. Beiträge zur Kenntniss der Zersetzungserscheinungen des Birkenholzes. Naturw. Ztschr. f. Forst- u. Landw., **2**: 393–406, figs. 1–7.

Molisch, Hans.

1888. Zur Kenntniss der Thyllen, nebst Beobachtungen über Wundheilung in der Pflanze. Sitzungsber. d. Ak. d. Wiss. [Vienna], Math. Naturw. Cl., **97**: 264–298, 2 pls.

Münch, Ernst.

1908. Die Blaufäule des Nadelholzes. Naturw. Ztschr. f. Forst- u. Landw., **5**: 531–573, 29 figs., 1907; **6**: 32–47, 3 figs.; 297–323, 2 figs., 1908. Abs. *in* Phytopath., **1**: 104. 1911.

1909. Untersuchungen über Immunität und Krankheitsempfanglichkeit der Holzpflanzen. Naturw. Ztschr. f. Forst- u. Landw., **7**: 54–75; 87–114; 129–160.

1910[1]. Versuche über Baumkrankheiten. Naturw. Ztschr. f. Forst- u. Landw., **8**: 389–408; 425–447; 18 figs.

1910[2]. Über krankhafte Kernbildung. Naturw. Ztschr. f. Forst- u. Landw., **8**: 533–547; 553–569, 2 figs.

Schrenk, Herman von.

1900. Some diseases of New England conifers. Div. Veg. Phys. and Path., U. S. Dept. Agr. Bul. **25**: p. 1–56, pl. 1–15, fig. 1–3.

1914: A trunk disease of the lilac. Ann. Missouri Bot. Gard, **1**: 252–262, 2 pls.

Stevens, William Chase.

1910. Plant anatomy from the standpoint of the development and functions of the tissues and handbook of microtechnique. 2nd Edition. 379 p., illus. Philadelphia.

Storer, F. H.

1898. Laboratory Notes. Bul. Bussey Institute, **2**: 409–421.

Temme, F.

1885. Über Schutz- und Kernholz, seine Bildung und physiologische Bedeutung. Landwirtsch. Jahrb., **14**: 465–484, pl. 6–7.

Thomsen, Th.

1879. Chemische Untersuchung über die Zusammensetzung des Holzes. Jour. f. praktische Chemie, N. F. **19**: 146–168.

Tubeuf, Carl F. von.

1886. *Cucurbitaria Laburni* auf *Cytisus Laburnum*. Bot. Centbl., **27**: 23–27.

1889. Über normale und pathogene Kernbildung der Holzpflanzen und die Behandlung der Wunden derselben. Ztschr. f. Forst- u. Jagdw., **21**: 385–392.

Tuzson, J.

1903. Anatomische und mykologische Untersuchungen über die Zersetzung und Conservierung des Rothbuchenholzes. Math. u. Naturw. Ber. aus Ungarn., 19: 242–282.

Will, Alfred.

1899. Beiträge zur Kenntniss der Kern- und Wundholzes. (Diss.), 92 pp., 3 pls., Bern.

Explanation of Plates.

Plate I.

Effect of *Pyropolyporus igniarius* (L.) Murrill upon a living tree. Cross section of the trunk of a silver maple (Acer saccharinum Linn.) which bore but one fruiting body, this being the only external indication of disease. Note the thin black zones surrounding the completely decayed wood; also the place of entrance of the fungus at the upper left-hand corner, produced by the rotting of a dead lateral branch. Photo by courtesy of the U. S. Bureau of Plant Industry.

PLATE I.

PLATE II.

Cross section of a sugar maple (*Acer saccharum* Marsh.) log rotted by *Elfvingia megaloma* (Lév.) Murrill., X ½. Notice the irregularity of the black zones surrounding the areas in various stages of decay. This irregularity is due to the decay starting simultaneously from several centers.

PLATE II.

Plate III.

The last portions of the sapwood of a hickory [*Hicoria glabra* (Mill.) Britton] log to be decomposed by the action of *Coriolus prolificans* (Fries) Murrill, the remainder of the sapwood being completely decayed. The completely disintegrated wood adhering to these comparatively sound pieces was removed by rubbing and scraping. Note the black color of the superficial portions of these pieces of undisintegrated wood. It was caused by the infiltration of abundant decomposition products into those portions immediately adjoining the completely decayed wood. The central piece (marked X) shows one of the pieces in transverse section.

Plate III.

Plate IV.

Fig. 1. Photomicrograph of a cross section of a portion of the sapwood of *Hicoria minima* (Marsh.) Britton rotted by *Coriolus prolificans* (Fries) Murrill, showing a black zone in cross section, X 100. The wood at the right has been thoroughly decayed as the appearance of the cell walls will testify. At the left the wood is in the earlier stages of decay and is giving rise to decomposition products upon the advance of the decay. In the center is shown a back zone which separates the portions of wood in the different stages of decay.

Fig. 2. Photomicrograph of a radial section of a portion of the sapwood illustrated in Plate III, showing the formation of the brown drops of the decomposition products in the pith ray cells, X 100. The photograph was made of a portion of wood lying approximately one-half cm. within the external infiltrated portion.

PLATE IV.

Plate V.

Camera lucida drawing of a pith ray illustrated in Plate IV, Fig. 2, showing in detail the formation of the brown drops of the decomposition products in the pith ray cells, X 650. Occasional fine fungal hyphae may be seen passing through the simple pits in the end walls of the pith ray cells.

PLATE V.

PLATE VI.

Coriolus prolificans (Fries) Murrill, on trunks of *Quercus coccinea* Muenchh. killed by a light surface fire. A two-foot rule is shown on the trunks. This photograph shows the general appearance and habit of growth of this extremely common sap-rotting fungus. It was principally the black zones of decomposition products formed in hickory wood as a result of its decay by this fungus that have been studied here.

PLATE VI.